

A SECTIONAL REVISION OF *LUDWIGIA* SECT. *MYRTOCARPUS* S. LAT. (ONAGRACEAE)¹

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ABSTRACT

Ludwigia sect. *Myrtocarpus* (Onagraceae), hitherto taken in an inclusive sense, is here divided into seven sections, all confined to or centering in South America. Four of these sections—*Amazonia* (*L. densiflora*), *Heterophylla* (*L. inclinata*), *Humboldtia* (*L. sedoides*), and *Tectiflora* (*L. latifolia*)—are monotypic and of uncertain relationship to one another and to the other portions of the genus, although it is possible that *Tectiflora* is related to one of the more generalized groups into which sect. *Myrtocarpus* is here divided. The remaining three sections, *Myrtocarpus* s. str., *Michelia*, and *Pterocaulon*, do seem to be interrelated to one another and to the ditypic African sect. *Africana*, but their similarity is based mainly upon their retention of generalized features. The least specialized section of the genus is sect. *Myrtocarpus* s. str., but the only section of this part of the genus in which genetic self-incompatibility is retained is sect. *Michelia*.

Ludwigia (Onagraceae), the only genus of the very distinctive tribe Jussiaeae, represents an evolutionary line separate from all other genera of the family (Raven, 1963, 1979; Eyde, 1977; Raven & Tai, 1979). It has some 80 species of pantropical distribution with some distinctive elements in temperate Eurasia and especially North America. Within this genus, the primarily South American sect. *Myrtocarpus* (Munz, 1942; Raven, 1963) has been the largest (with 23 species) and most heterogeneous.

In the light of my recent biosystematic investigations, it now appears that *Ludwigia* sect. *Myrtocarpus*, in the traditional sense, is a partly artificial group, some elements of which are held together only by their common possession of a series of plesiomorphic characteristics ("a preponderance of ancestral features," Eyde, 1978). These are primarily the unspecialized capsules with their pluriseriate ovules and narrow raphe. Data from artificial hybridization and a more detailed morphological study than was possible earlier has resulted in the detection of seven distinct groups within what has been regarded as sect. *Myrtocarpus*, each comparable with the 16 other sections of *Ludwigia* (Raven, 1963), as well as with the kind of relatively close-knit, presumably monophyletic sections that have been utilized in the classification of other genera of the family (e.g., Lewis & Lewis, 1955; Raven, 1969, 1976). Although the sections *Myrtocarpus* s. str., *Michelia*, and *Pterocaulon* as recognized in this paper are probably directly related to one another and to the ditypic African sect. *Africana* (Raven, 1963), they are sharply distinct morphologically, and it has not been possible to obtain artificial hybrids between them. The sections which I recognize for the species included by Raven (1963) in sect. *Myrtocarpus*, and their principal included species, are as follows:

Ludwigia* sect. *Myrtocarpus (Munz) Hara, J. Jap. Bot. 28: 291. 1953. Based on *Jussiaea* sect. *Myrtocarpus* Munz, Darwiniana 4: 184. 1942.

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Type species: *L. peruviana* (L.) Hara.

Perennials. Sepals 4–5(–6). Petals 4–5(–6). Stamens 8–10(–12). Capsule thin walled, 4-angled to terete, irregularly dehiscent. Seeds oblong, sometimes curved. Self-compatible.

Included species: *Ludwigia bullata* (Hassler) Hara, *L. burchellii* (Mich.) Hara, *L. caparosa* (Camb.) Hara, *L. elegans* (Camb.) Hara, *L. foliobracteolata* (Munz) Hara, *L. laruotteana* (Camb.) Hara, *L. peruviana* (L.) Hara, *L. sericea* (Camb.) Hara, *L. tomentosa* (Camb.) Hara.

Ludwigia sect. **Michelia** T. P. Rammamorthy, sect. nov.

Type species: *L. nervosa* (Poir.) Hara.

Herbae perennes. Sepala 4. Petala 4. Stamina 8. Capsula pariebus relative tenuibus, plus minusve 4-angulata, teres vel suburceolata, irregulariter dehiscens. Semina oblonga curvata.

Included species: *Ludwigia anastomosans* (DC.) Hara, *L. brachyphylla* (Mich.) Hara, *L. myrtifolia* (Camb.) Hara, *L. nervosa* (Poir.) Hara, *L. rigida* (Miq.) Sandwith.

This section consists mainly of large woody plants, essentially shrubs, in which genetic self-incompatibility predominates. The name commemorates M. Micheli (1844–1902), who prepared the important treatment of “*Jussiaea*” for Martius’s *Flora Brasiliensis* (1875).

Ludwigia sect. **Pterocaulon** T. P. Ramamoorthy, sect. nov.

Type species: *L. erecta* (L.) Hara.

Herbae annuae. Caules manifeste 4-angulati melius alati. Sepala 4. Petala 4. Stamina 8. Capsula relative pariebus relative tenuibus, conspicue 4-angulata anguste alata, irregulariter dehiscens. Semina oblonga exigue curvata.

Included species: *Ludwigia decurrens* Walt., *L. erecta* (L.) Hara, *L. longifolia* (DC.) Hara, *L. mexiae* (Munz) Hara.

This section consists of subglabrous, weedy, self-pollinating, mostly annual species that are clearly distinct from but likely derived from plants similar to those included in sect. *Michelia*. The name of the section refers to its 4-angled or 4-winged stems and capsules.

Ludwigia sect. **Tectiflora** T. P. Ramamoorthy, sect. nov.

Type species: *L. latifolia* (Benth.) Hara.

Herbae vel frutices erectae. Sepala 4. Petala 4. Stamina 8. Contextus sporogenous antherae in loculis subdivisus; antherae pilis longis vestitae. Capsula pariebus crassis subtarde dehiscens subglobosa. Semina oblongo-obovoidea.

Only species: *Ludwigia latifolia* (Benth.) Hara.

This species shares with the completely unrelated *L. linearis* Walt. the distinction of being the only member of the genus *Ludwigia* in which the sporogenous tissue of the anthers is divided into packets longitudinally by sterile tissue, as in *Hauya* and four genera of the tribe Onagreae, *Clarkia*, *Heterogaura*, *Gaura*, and *Calylophus*. It is apparently the only member of the genus, and perhaps also

of the family, with pubescent anthers. The sectional name refers to the fact that the flowers are more or less hidden at the bases of the subtending leaves.

Ludwigia sect. **Heterophylla** T. P. Ramamoorthy, sect. nov.

Type species: *L. inclinata* (L.f.) Raven.

Herbae aquaticae caulibus natantibus ad nodos radicanibus. Folia basalia (saepe submersa) verticillata 4 ad eadam nodam; folia superiora alternantia latiora. Sepala 4. Petala 4. Stamina 4 vel 8. Capsula pariebus relative tenuibus, irregulariter dehiscens, aliquantum 4-angulata. Semina oblonga recta.

Only species: *Ludwigia inclinata* (L.f.) Raven.

This is a very distinctive species of uncertain affinities. In no other species of the genus are the lower leaves whorled. *Ludwigia verticillata* Munz, originally assigned to sect. *Dantia*, refers to a form of this species in which the epipetalous anthers have been lost; P. H. Raven (pers. comm.) has studied populations in marshy places on the Isthmus of Tehuantepec in Oaxaca, Mexico, in which plants with 4 stamens occur intermingled with others with 8 stamens, and are indistinguishable otherwise. As in many aquatic species, the morphology is highly variable, and the name *Ludwigia potamogeton* (Buchell ex Mich.) Hara, here relegated to synonymy, has been used to refer to plants with somewhat narrower leaves and less inflated stems. This species is primarily autogamous and is the only one in the genus in which two types of leaf arrangement occur, whence the sectional name.

Ludwigia sect. **Humboldtia** T. P. Ramamoorthy, sect. nov.

Type species: *L. sedoides* (Humb. & Bonpl.) Hara.

Herbae aquaticae caulibus natantibus ad nodos radicanibus. Folia integra rosula terminalia conferta. Sepala 4. Petala 4. Stamina 8. Capsula pariebus tenuibus 4-angulata irregulariter dehiscens. Semina obovoidea curvata.

Only species: *Ludwigia sedoides* (Humb. & Bonpl.) Hara.

This is a most attractive species, with its beautiful symmetrical floating rosettes and large yellow flowers. It is probably mainly self-pollinating, since the anthers surround the stigma, but I have no direct information on this point. Its affinities within *Ludwigia* are obscure. The section is dedicated to the memory of that intrepid explorer of Latin America, Alexander von Humboldt (1769–1859), who first discovered it in Colombia and later described it.

Ludwigia sect. **Amazonia** T. P. Ramamoorthy, sect. nov.

Type species: *L. densiflora* (Mich.) Hara.

Herbae annuae erectae. Flores spica brevo dispositi. Sepala 4–6. Petala 4–6. Stamina 8–12. Capsula pariebus crassis lineatis tarde dehiscens teres ad extremos angustata. Semina oblonga recta.

Only species: *Ludwigia densiflora* (Mich.) Hara.

This remarkable highly self-pollinating species is the only member of the genus that is confined to the Amazon Basin, whence the sectional name. Its capsular morphology is without parallel in the genus, the strong ribs and very tardy de-

hiscence being unique. The variability in flower part number may suggest a relatively great antiquity for the evolutionary line leading to this species, despite the evident specializations in the habit and the morphology of the capsule.

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